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AN APPARENTLY NEW FAMILY OF AMBLYPOD MAMMALS FROM MONGOLIA[1]

By Walter Granger and William K. Gregory

The three incomplete fossil lower jaws and a last lower molar which are the subjects of this note were found by members of the Central Asiatic Expedition of 1925 and 1928 in the Shara Murun region of Inner Mongolia. By preliminary field and laboratory determinations they had been referred tentatively to the chalicothere branch of the Perissodactyla, but later a direct comparison with the known Mongolian chalicotheres by Mr. Edwin H. Colbert revealed many significant differences that will be referred to later in this report. The tentative removal of these specimens from the chalicotheres initiated a series of rejections by different members of the departmental staff which progressively enhanced the interest and possible importance of these specimens. Dr. George Gaylord Simpson could recall no group among all the hosts of extinct South American ungulates in which the orphans could find a home; the present authors unanimously shut the gates of the known perissodactyls and then by systematic comparisons eliminated one family after another of artiodactyls. Nor did we neglect to consider even the insectivores and bats for analogies with the peculiar characters of the dentition revealed by the present specimens. It was not until we began to make comparisons with the Paleocene group of Taligrada, as represented especially by *Titanoides* and *Pantolambda*, that we noted resemblances to our specimens that had the appearance of being more than mere convergences or parallelism.

The conclusion that the specimens under consideration represent a family of mammals new to science may now be set forth.

In the first place we can be sure that we are dealing with a placental mammal of some sort from the fact that the dental formula: I_3, C_1, P_4, M_3, is the classic primitive eutherian formula. Hence by even the most conservative application of the axiom of the irreversibility of evolution we may eliminate not only all pre-placental but also all those placental genera in which the dental formula has become either reduced or second-

[1]Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution No. 125.

arily increased beyond the primitive placental grade. Secondly, we can eliminate all forms that show advanced specialization of the dentition by the fact that in our specimens even the posterior premolars are still in

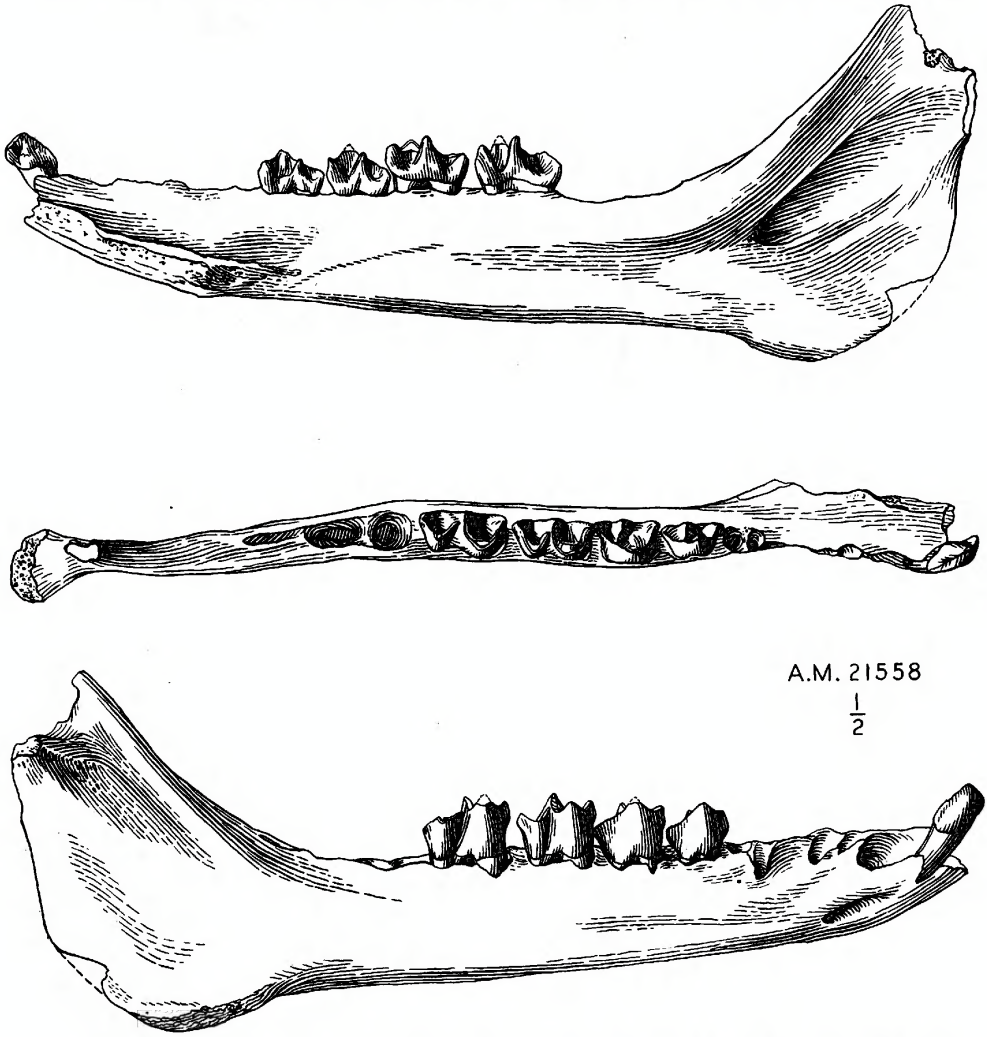

Fig. 1. *Pantolambdodon inermis*, gen. et sp. nov. Type, Amer. Mus. No. 21558. The right ramus of the lower jaw: inner, superior and outer views. One-half natural size.

a relatively low stage of complication, while the molars, although advanced beyond the primitive tuberculo-sectorial stage, have not assumed any of the specializations that are characteristic of the various families of perissodactyls and artiodactyls, as will be shown in detail later.

Relationship with any of the more typical South American ungulates is eliminated by the absence in the present specimens of the various queer diagnostic characters of these heterodox non-conformists. For instance, the posterior V of the present forms lacks the isolated entoconid of many notoungulates, and there is no flattening or asymmetrical enlargement of the talonid ectoloph. *Trigonostylops*, as described by Simpson (Amer. Mus. Novitates No. 608, 1933) has wide diastemata on either side of P_1 and its molars have large talonids and more or less separate entoconids. *Palaeostylops*, a supposed relative of the notoungulates found in the Gashato Paleocene of Mongolia, has the excessively flattened talonid ectoloph on M_3 and distinct entoconid crest, which are conspicuously lacking in our specimens.[1] Among the litopterns the Macraucheniidae agree with our forms in the dental formula and in having completely W-shaped lower molar crowns, but differ radically in that the talonid is larger than the trigonid and the premolars are much more complex. The horse-like litopterns also have complex premolars and other striking specializations.

Our lower jaws differ from those of chalicotheres in that their premolars are all essentially of one pattern, with very small incipient talonid fossae, whereas in chalicotheres the talonid of P_4 is larger than the trigonid. In the molars also the talonids are much smaller than the trigonids, while in chalicotheres the talonids, at least on M_1 and M_2, are somewhat larger than the trigonids. The diastemata, front teeth, and general shape of jaw are widely different.

It may be stated summarily that neither *Lambdotherium* nor the true titanotheres[2] offer the slightest suggestion of relationship with the specimens in hand, and the same is true of all the tapirs, horses, rhinoceroses, etc., with lophodont molars of various kinds.

The artiodactyls present a more extensive problem, but after fairly wide comparisons we may eliminate at once all the bunodont pigs, peccaries and entelodonts and all the selenodonts high and low from *Anoplotherium* to *Xiphodon*, and from *Agriochoerus* to *Vishnutherium*. The reasons are that in the artiodactyls, even in the most primitive Lower Eocene dichobunids, the paraconids are absent or inconspicuous and the molar cusps are antiodont, that is, they are grouped in two pairs, the metaconid being directly internal to the protoconid and the entoconid to the hypoconid, whereas in the present specimens the lower molar

[1] Matthew, W. D., Walter Granger, and George Gaylord Simpson, 1929. Amer. Mus. Novitates, No. 376, p. 1.

[2] Osborn, H. F. 1929. 'The Titanotheres of Ancient Wyoming, Dakota, and Nebraska.' Monograph 55, U. S. Geol. Surv.

cusps conform to the amoebodont pattern of Cope,[1] since the paraconid is elevated and the metaconid and entoconid lie well behind the proto- and hypoconids respectively. Moreover in the artiodactyls the talonid is at least not inferior in width to the trigonid, whereas in the present specimens the reverse is the case. Nor do the premolars of artiodactyls agree in details with those of the Mongolian jaws. Hence the vague

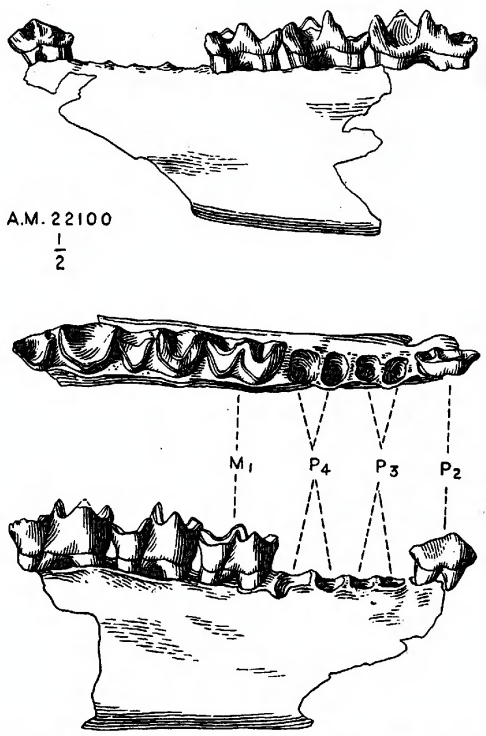

Fig. 2. *Pantolambdodon inermis*, gen. et sp. nov. Paratype, Amer. Mus. No. 22100. Fragment of the right ramus of the lower jaw: inner, superior and outer views. One-half natural size.

resemblances to the artiodactyls found in the elongate jaw, backwardly sloping weak coronoid process, and possibly spatulate front teeth of our specimens, are merely convergent.

The recent hyracoids need not detain us, while the Egyptian hyracoids figured by C. W. Andrews[2] have nearly molariform premolars and primitive perissodactyl-like molars.

[1]Cope, E. D. 1874. 'On the Homologies and Origin of the Types of Molar Teeth of Mammalia Educabilia.' Journ. Acad. Nat. Sci. Phila., (2) VIII, Part I, Art. III, pp. 71–89, 29 figs.

[2]Andrews, C. W. 1906. 'Descriptive Catalogue of the Tertiary Vertebrata of The Fayûm, Egypt.' British Museum (N.H.). Pl. VI.

The various families of Condylarthra as revised and figured by Matthew and Granger[1] seem to bring us a step nearer to the possible point of origin of our specimens, since at least the older Condylarthra stand fairly near the foci of the numerous ungulate groups. The bunodont condylarths including *Protogonodon* and *Phenacodus* are eliminated from close relationship by the emphasis of the talonid and reduction or absence of the paraconid. In *Ectocion* the crista obliqua, connecting the hypoconid with the base of the metaconid, is inclined anteroposteriorly and the molar pattern is suggestive of the primitive perissodactyl type, but not of the V-shaped configuration of the Mongolian molars; the talonid of P_4 in *Ectocion* is already submolariform and widely different from that of our specimens. The lower molars of meniscotheres have sharply reduplicate metaconids and fairly wide talonids; their P_4 is submolariform. In the Hyopsodontidae, on the other hand, the talonids are distinctly wider than the trigonids and hypoconulids are retained on the molars. These may well be primitive characters for all protoungulates. The premolars also are relatively primitive. In short, it might be rash to affirm that the Mongolian forms were not derived from primitive hyopsodonts, but all the closer resemblances, as we shall see, do not favor such a derivation.

The Dinocerata are excluded by their lophodont molar patterns, to say nothing of other high specializations. In the coryphodonts the lower premolars, on the other hand, approach our Mongolian type and even the molars include two V's. Moreover, definitive coryphodonts were contemporary with our specimens.[2]

Passing to the Taligrada we note that the smaller Periptychidae, including *Anisonchus*, are far more primitive, according to accepted standards, than the Mongolian fossils, since *Haploconus, Conacodon* and *Anisonchus* have simpler premolars and very primitive bunodont lower molars, with well developed normal talonids. This is true even of *Periptychus*. Also these forms have more primitive, shorter, stouter jaws with wider, lower ascending rami. In other words, they are all far nearer to the primitive insectivore-creodont central placental type.

When we come to *Pantolambda* and *Titanoides*, however, we find some apparently reliable indications of remote relationship to the Mongolian types, especially in the form of the premolars and molars. In spite of the fact that *Titanoides* is a graviportal form almost as big as

[1]Matthew, W. D. 1915. Bull. Amer. Mus. Nat. Hist., XXXIV, pp. 311–328.
Granger, Walter. 1915. Bull. Amer. Mus. Nat. Hist., XXXIV, pp. 329–361.
[2]Osborn, Henry Fairfield, and Walter Granger. 1932. 'Coryphodonts and Uintatheres from the Mongolian Expedition of 1930.' Amer. Mus. Novitates, No. 552, pp. 1–16.

Coryphodon,[1] it shares the following features with the Mongolian fossils: (1) Dental formula of primitive placental type; (2) P_1, P_2 compressed; (3) talonid fossa of premolars formed between the posterior ridge connected with the main cone and a transverse metaconid ridge; (4) molar talonids with V-shaped crests; (5) talonid of M_3 narrower than trigonid; (6) M_3 with reduced or no hypoconulids; (7) M_1, M_2 with no trace of hypoconulid; (8) molars not crowded but slightly spaced; (9) coronoid process inclined backward. *Titanoides* is distinguished from the Mongolian forms by its relatively gigantic size, powerful, more erect incisors and canines; relatively shorter, more massive jaw, etc.

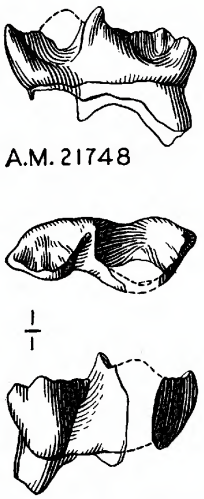

Fig. 3. *Pantolambdodon inermis*, gen. et sp. nov. Paratype, Amer. Mus. No. 21748. Last right lower molar; inner, superior and outer views. Natural size.

From *Pantolambda* the present form differs in its much more elongate slender jaw, somewhat procumbent front teeth, more hypsodont cheek teeth, compressed premolars; the molars have much larger anterior V's and smaller posterior V's; the ascending ramus slopes backward and is distinctly delicate.

In short, reference to the Amblypoda is indicated by the primitive dental formula, and especially by the peculiar mode of complication of P_2-P_4 and by the progressive character of the molar trigonids and narrowness of the talonids. That the Mongolian forms represent a new family of Amblypoda seems probable in view of the differences above noted.

Order **AMBLYPODA**

Family **Pantolambdodontidae**, fam. nov.

Dental formula: I_3, C_1, P_4, M_3; cheek teeth incipiently hypsodont; premolars compressed, two-rooted, P_2-P_4 with incipient talonid fossa formed between posterior crest of main cusp and sharp metaconid ridge; P_2-P_4 with well developed trigonid V and incipient talonid V; molars with high trigonid V, and lower, smaller talonid V, trigonid cusps unusually high and pointed; trigonid and talonid basins remarkably deep, a sharp oblique crease on the buccal side running behind the trigonid and crowding the talonid, ending at the top of the talonid root; hypo-

[1]Patterson, Bryan. 1934. 'A Contribution to the Osteology of *Titanoides* and the Relationships of the Amblypoda.' Proc. Amer. Phil. Soc., LXXIII, No. 2, pp. 71–101.

conulid absent on M_1 and M_2, vestigial on M_3; lateral incisor spatulate, mandible long and relatively slender, coronoid inclined backward, angular region rounded without distinct process.

Pantolambdodon, gen. nov.

Genotype P. *inermis*

Generic characters not certainly separable from family characters.

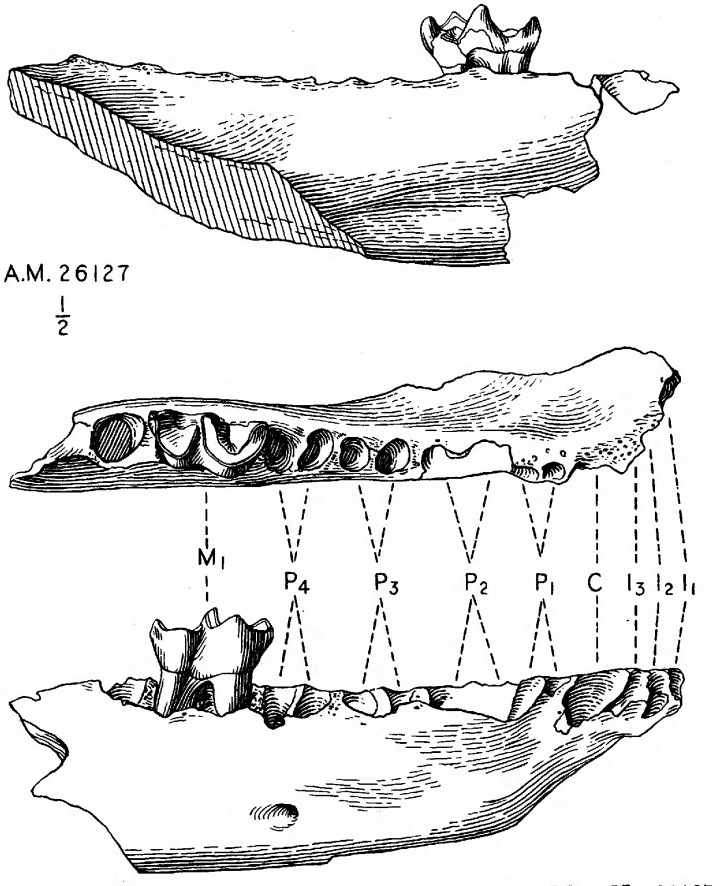

Fig. 4. *Pantolambdodon fortis*, sp., nov. Type, Amer. Mus. No. 26127. Fragment of right ramus of lower jaw: inner, superior and outer views. One-half natural size.

Pantolambdodon inermis, sp. nov.

TYPE.—A. M. No. 21558. Lower jaw, right ramus, with I_3 r. and P_3-M_2, alveoli of all other teeth.

PARATYPES.—A. M. No. 22100. Fragment of right ramus of lower jaw with P_2 and M_{1-3}. A. M. No. 21748. A last molar of the right side.

LOCALITY.—Eight miles north of Tukhum Lamasery (Chimney Butte). Shara Murun region, Inner Mongolia, 1925.

HORIZON.—Ulan Shireh beds (=Irdin Manha), Upper Eocene.

SPECIFIC CHARACTERS.—Size small, depth of jaw below M_2, 29–36; M_1 a. p. x tr. (crown), 20×9.5—20×11 mm.

Pantolambdodon fortis, sp. nov.

TYPE.—A. M. No. 26127, fragmentary right ramus of lower jaw with M_1 and alveoli of all anterior teeth.

TYPE LOCALITY.—Eight miles north of Tukhum Lamasery (Chimney Butte), Shara Murun region, Inner Mongolia, 1928.

HORIZON.—Ulan Shireh beds (=Irdin Manha), Upper Eocene.

CHARACTERS.—Differing from *P. inermis*, so far as observable, only by its larger size and relatively more massive jaw. See table of measurements.

Measurements of *Pantolambdodon*

	P. inermis No. 21558 Type	*P. inermis* No. 22100 Paratype	*P. inermis* No. 21748 Paratype	*P. fortis* No. 26127 Type
Lower jaw, incisive border to post. border	230			
Depth of jaw below M_2	29	36		48 e.
M_1 to M_3	71 e.	67		
P_1 to P_4	67			
P_2 a.p. × tr. (crown)		16 ×6.5		
P_3 a.p.× tr. (crown)	15 × 8			
P_4 a.p. × tr. (crown)	16 ×10			
M_1 a.p. × tr. (crown)	20 × 9.5	20 ×11		29×13
M_2 a.p.× tr. (crown)	21.5×11	22.7×11.5		
M_3 a.p. × tr. (crown)		26 ×11.5	23 × 9	
M_1 trigonid a.p. × tr.	11.5× 9	11 ×10		16 ×13.5
M_1 talonid a.p. × tr.	8.5× 9	9 ×10		12.5×13
M_2 trigonid a.p. × tr.	11.5× 9.5	13 ×10.5		
M_2 talonid a.p. × tr.	10 × 9	9.5× 9.5		
M_3 trigonid a.p. × tr.		15 ×11	12.5× 9.5	
M_3 talonid a.p. × tr.		11 × 8	11 × 7	

All measurements in millimeters.